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 KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon.—*Ann. Mag. nat. Hist.* (13) 2: 309–320.
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 THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269–270. Jena: Fischer.—*Denkschr. med.-naturw. Ges. Jena* 16: 269–270.

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NOTES ON THE ADDUCTOR JAW MUSCULATURE
OF *VENJUKOVIA*, A PRIMITIVE ANOMODONT
THERAPSID FROM THE PERMIAN OF THE U.S.S.R.

By

HERBERT R. BARGHUSEN

Cape Town

Kaapstad

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OF THE U.S.S.R.

By

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(With 4 figures)

[MS accepted 9 March 1976]

ABSTRACT

The primitive anomodont *Venjukovia*, from Zone II of the Russian Permian, has been thought to bridge the morphological gap between dinocephalians and dicynodonts. Much of the pattern of adductor jaw musculature in *Venjukovia* conforms closely to that found in dicynodonts and is thereby consistent with the hypothesis that these are closely related forms. The most important similarity is the probable presence in *Venjukovia* of a distinctive lateral division of the external adductor. The presence of this division is a derived character previously known only in dicynodonts. However, as far as can be determined, similarities between *Venjukovia* and dinocephalians only involve joint possession of a primitive therapsid arrangement of various other parts of the jaw musculature. Therefore, the muscle pattern does not provide evidence of a closer relationship with dinocephalians than with other primitive therapsid groups. Moreover, in contrast to primitive dinocephalians (brithopodids), *Venjukovia* lacks an extensive area of origin of the external adductor from the dorsal surface of the temporal roof. The absence of this specialized area of origin suggests (tentatively) that *Venjukovia* retained the primitive therapsid condition of the temporal roof and that the lines leading to *Venjukovia* and dicynodonts on the one hand and to dinocephalians on the other diverged before the primitive dinocephalian condition was achieved.

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INTRODUCTION

The Russian anomodont *Venjukovia* has long attracted attention because it shows structural resemblances to tapinocephalid dinocephalians on the one hand (Efremov 1940) and to dicynodonts on the other (Watson 1942, 1948). Efremov noted general resemblances between *Venjukovia* and tapinocephalids in the structure of the teeth, face and palate. Watson agreed but also noted that the lower jaw of *Venjukovia* shows many features which are, in essence, identical with those in dicynodonts. Romer (1956) regarded *Venjukovia* as seeming to bridge the morphological gap between dinocephalians

and dicynodonts. It is not the purpose of this paper to extensively analyse the phylogenetic position of *Venjukovia*; the issues involved are complex and demand a thorough phylogenetic analysis of therapsids in general which is the subject of a paper in preparation. However, the present study, which involves a partial reconstruction of adductor jaw musculature in *Venjukovia*, has obvious potential for defining character states useful in such an analysis. In addition, some general but very tentative conclusions concerning the possible relationships between *Venjukovia*, dinocephalians and dicynodonts can be advanced based on a comparison of their patterns of adductor jaw musculature. Accordingly, such comparisons will be made in so far as it is possible to do so in this paper.

A rationale for jaw muscle reconstruction in synapsid reptiles and a reconstruction of this musculature (based on a reptilian model) in the pelycosaur *Dimetrodon* has already been provided (Barghusen 1973). The evaluation of direct evidence of muscle attachment as well as the arguments concerning the distribution of individual jaw muscles presented for *Dimetrodon* also apply to the reconstructions made here. For this reason, the reader is referred to Barghusen (1973) for clarification of the issues involved. In addition, by virtue of the phylogenetic position of *Dimetrodon* within the pelycosaur family from which therapsids were derived, the pattern of jaw musculature which it shows constitutes the pattern primitive to the evolution of this musculature in therapsid reptiles. Therefore, comparisons of the reconstructed musculature in *Venjukovia* will also be made with that of *Dimetrodon* exemplifying the pre-therapsid arrangement from which the musculature of *Venjukovia* was derived.

MATERIAL

The reconstruction of adductor jaw musculature presented here for *Venjukovia* is based on information gained from a skull of *V. prima* (PIN 2793/1) and three lower jaws of *V. invisa* (PIN 157/1111, 157/1112, 157/5) housed in the Palaeontological Institute, U.S.S.R. Academy of Sciences, Moscow. The skull is exceptionally well-preserved except posteriorly where much of the bone forming the posterior margin of the lateral temporal fenestra, the posterior root of the zygomatic arch, and the occiput has flaked from the matrix. Nevertheless, the bone which is present, and impressions of bone in the matrix, clearly indicate that the outlines of the lateral temporal fenestra, temporal fossa, zygomatic arch, and the position of the quadrate correspond to that shown in Figures 1A and 1C. Matrix has not been cleared from the temporal fossae or the orbits. For this reason it is impossible to estimate the area of origin of m. adductor mandibulae internus pseudotemporalis, m. adductor posterior, and, if present, m. adductor mandibulae internus pterygoideus anterior. Consequently, these muscles will not be considered in this reconstruction. However, the medial surface of the lower jaw (Fig. 1D) has not departed sufficiently from that of *Dimetrodon* to suggest that the general areas

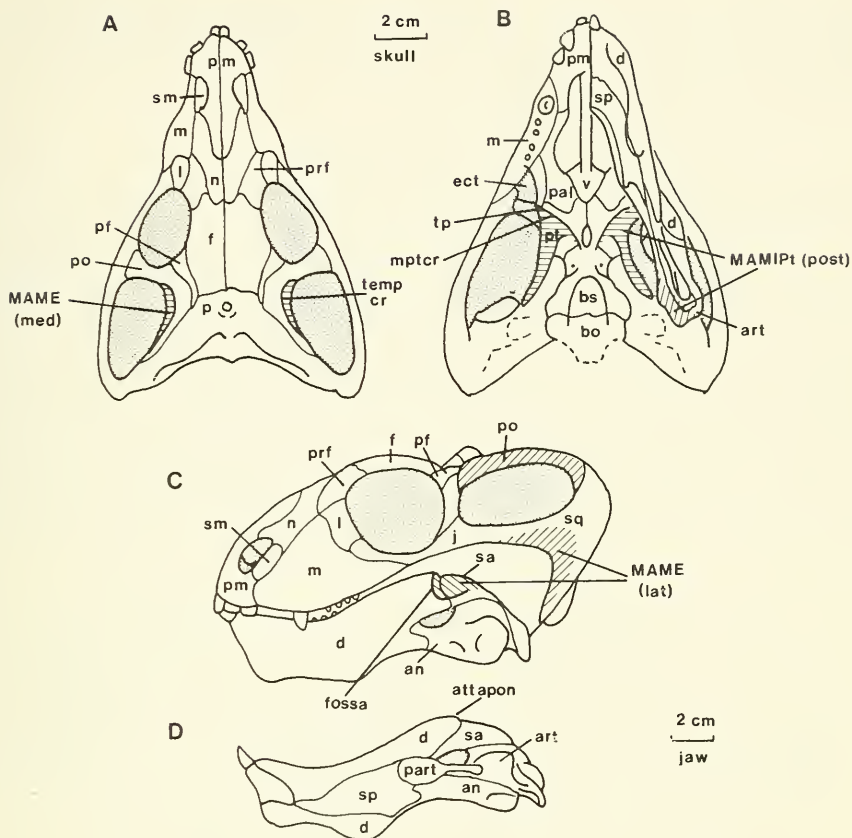


Fig. 1. Reconstruction of the skull and lower jaw of *Venjukovia*.

A. Dorsal view of skull. B. Ventral view of skull with left lower jaw in place. C. Lateral view of skull and lower jaw. D. Medial view of lower jaw. The areas of origin and insertion of the external adductor and posterior pterygoideus jaw musculature are indicated by parallel lines. The outline of the posterior margin of the skull and the position of the quadrate were determined from bone impressions in the matrix. (Skull reconstructed from PIN 2793/1; lower jaw reconstructed from PIN 157/1111, 157/1112, 157/5.)

of insertion of these muscles were significantly different from those in *Dimetrodon*.

The reconstruction of brithopodid jaw musculature is also based on specimens housed in the Palaeontological Institute, Moscow. These include an exceptionally well-preserved skull and lower jaw of *Titanophoneus potens* (PIN 157/1). Details of the temporal fossa were also gained from *Notosyodon gusevi* (PIN 2505/1).

Much of the information upon which the reconstruction of musculature in *Lystrosaurus* is based was collected in 1965 at Yale University from an acid-prepared skull (SAM-4325). Unfortunately this skull was subsequently

destroyed in transit. More recently, information has also been gained from acid-prepared material examined while the author visited the South African Museum, Cape Town. This material included a skull and lower jaw of *L. declivis* (Nat. Mus. C 403).

ADDUCTOR JAW MUSCULATURE

M. ADDUCTOR MANDIBULAE EXTERNUS

The temporal region of *Venjukovia* exhibits the posterodorsal enlargement of both the lateral temporal fenestra and temporal fossa which is characteristic of most therapsids as opposed to sphenacodontid pelycosaur (cf. Figs 2A, C). In dorsal view (Fig. 1A) the temporal fossa is broadly exposed due to the extensive but as yet incomplete reduction in the width of the temporal roof. The degree of reduction is comparable to that seen in some dicynodonts (cf. *Emydops*, Crompton & Hotton 1967, Fig. 1B) but not as extensive as that found, for example, in *Lystrosaurus* (Fig. 3A). The presence of a temporal crest (Fig. 1A, temp cr) in *Venjukovia* provides direct evidence that the external adductor took origin from the lateral face of that part of the postorbital forming

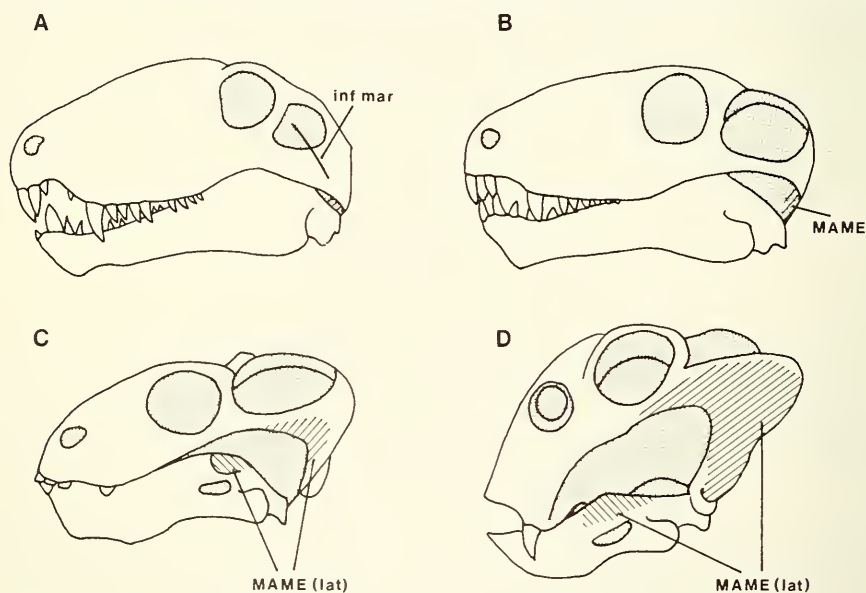


Fig. 2. Lateral views of the skull and lower jaw of *Dimetrodon*, A, hypothetical condition, B, *Venjukovia*, C, and *Lystrosaurus*, D, forming a morphological series which illustrates stages in the development of the lateral division of the external adductor jaw musculature characteristic of dicynodonts. In A the zygomatic arch is positioned close to the adducted lower jaw. In B the zygomatic arch is dorsally displaced creating an access route for that part of the external adductor originating from the anterior face of the quadratojugal and quadrate to invade the lateral surface of the squamosal. In C and D the arch is further displaced and the invasion, creating the lateral division of the external adductor, has taken place; in addition, an area of insertion for the lateral division is established on the dorsolateral surface of the lower jaw. (A after Romer and Price.)

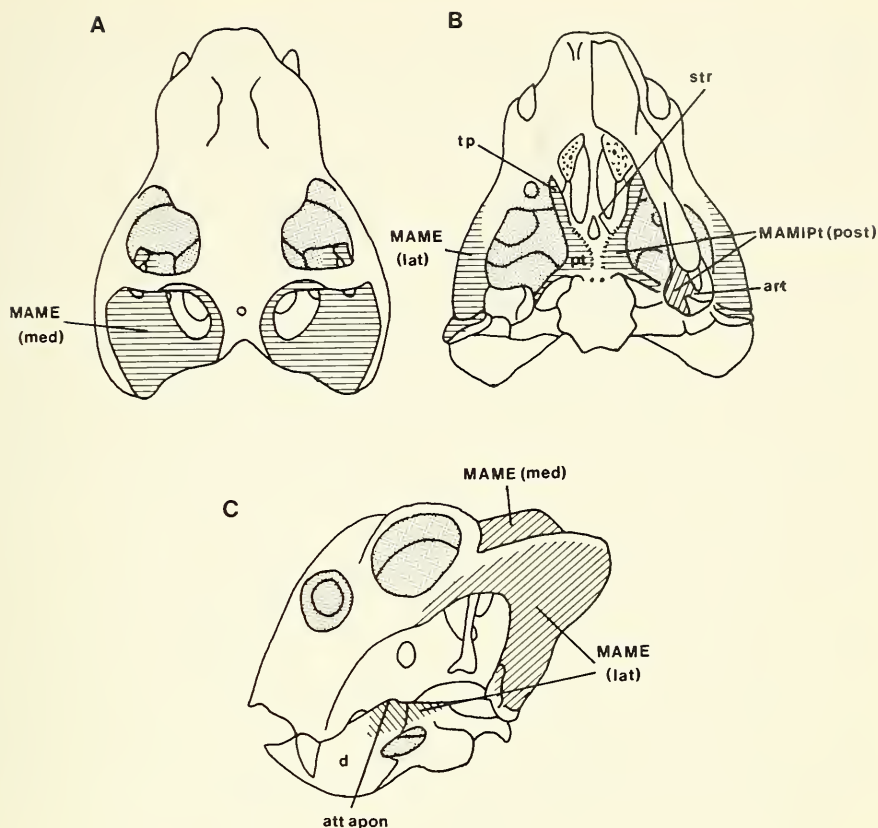


Fig. 3. The skull and lower jaw of *Lystrosaurus*.

A. Dorsal view of skull. B. Ventral view of skull with left lower jaw in place. C. Lateral view of skull and lower jaw. The areas of origin and insertion of the external adductor and posterior pterygoideus muscles are indicated by parallel lines.

the lateral margin of the temporal roof. The establishment of muscle origin here probably represents an invasion of muscle attachment from the anterior face of that part of the squamosal forming the posterior wall of the temporal fossa. This condition, which is a distinct departure from that found in sphenacodontids, was probably common among primitive therapsids as it is also found in gorgonopsids, *Biarmosuchus*, and *Eotitanosuchus* (personal observations). The extent of this muscle attachment on the postorbital also approaches that seen in dicynodonts (e.g. *Lystrosaurus*, Fig. 3A; also see Crompton & Hotton 1967; Cluver 1975). *Venjukovia*, however, does not achieve the specialized condition seen in brithopodids, the most primitive known dinocephalians. In brithopodids, the external adductor took extensive origin from the dorsal surface of the temporal roof (Fig. 4A; also see Watson 1948; Olson 1962; Boonstra 1963; Barghusen 1973). The condition in brithopodids contrasts

sharply with that found in other primitive therapsids (i.e. gorgonopsids, *Eotitanosuchus*, *Biarmosuchus*, and ictidorhinids) as well as in *Venjukovia*. All these animals retain the sphenacodontid arrangement, in which no adductor jaw musculature attaches to the dorsal surface of the temporal roof. In contrast to more primitive dinocephalians, many tapinocephalid dinocephalians (e.g. *Moschops*) reverted back to the primitive therapsid and sphenacodontid arrangement in the sense that the attachment of the external adductor to the dorsal surface of the temporal roof was eliminated. Evidence strongly suggests that this reversal in tapinocephalids was related to the development of head-butting behaviour in these animals (Barghusen 1975). Conceivably a reversal may also have taken place in the ancestry of *Venjukovia*. However, *Venjukovia* does not exhibit any of the specializations for use of the dorsal surface of the head in butting which are displayed by tapinocephalids and which, if present in *Venjukovia*, would suggest tapinocephalid relationships. At the moment it seems more likely, therefore, that the condition manifested by *Venjukovia* is a retention of the primitive therapsid and pelycosaur condition as there are no obvious functional reasons to suggest that the absence of muscle attachment to the dorsal surface of the temporal roof was secondarily derived. If so, *Venjukovia* reflects a morphological stage, with regard to the attachment of part of the adductor musculature, resembling that which must have been antecedent to the stage reached by the most primitive known dinocephalians. Such a conclusion appears to be implicit in Boonstra's (1963) remarks to the effect that when the dinocephalian and dicynodont lines diverged, the intertemporal skull table was broad and the origin of the adductor muscles showed a fairly primitive condition. This conclusion runs counter to suggestions (Efremov 1940) that *Venjukovia* was derived from tapinocephalids.

Preparation of the temporal fossa is not complete in the skull of *Venjukovia*. However, there are reasons to believe that the undersurface of much of the retained portion of the temporal roof served for the attachment of the external adductor. This is expected from the distribution of the attachment of this muscle in living reptiles. In addition, a depression on the undersurface of the roof indicates that this was the case in *Dimetrodon* (see Barghusen 1973) and a similar scar or depression has been found in all therapsids examined in which the temporal region was sufficiently prepared and which showed a degree of development of the temporal roof similar to that of *Venjukovia*. These therapsids include *Titanophoneus* (see Orlov 1958, fig. 21) and *Notosyodon* among the dinocephalians and *Leontocephalus* (see Kemp 1969, fig. 5) among the gorgonopsids. This evidence clearly suggests that such an arrangement of muscle attachment was present prior to and during the evolution of those therapsids that did not completely eliminate the temporal roof. It is also expected (Barghusen 1973) that the dorsal and ventrolateral parts of the posterior wall of the temporal fossa, including the squamosal and quadrate, served as an area of origin of the external adductor muscle in *Venjukovia*. The squamosal portion of this area of attachment to the posterior wall of the fossa would have served

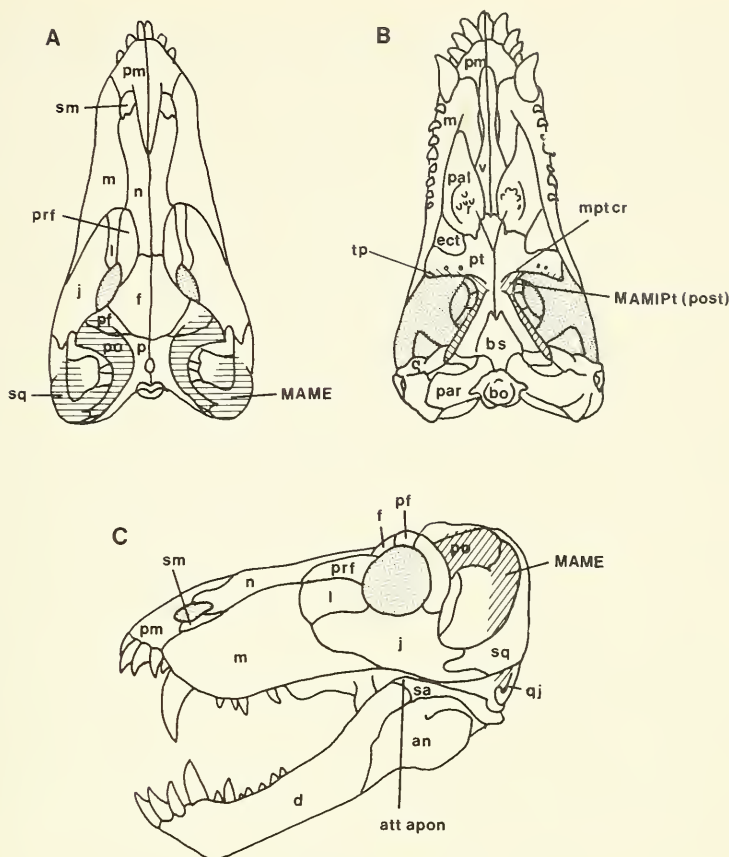


Fig. 4. The skull and lower jaw of *Titanophoneus*.

A. Dorsal view of skull. B. Ventral view of skull. C. Lateral view of skull and lower jaw. The areas of origin of the external adductor and posterior pterygoideus muscles are indicated by parallel lines. (Outlines after Orlov.)

as the original site from which the invasion of muscle attachment onto the lateral surface of the postorbital in therapsids, including *Venjukovia*, took place.

The posterodorsal tip of the dentary, forming the apex of the coronoid eminence in *Venjukovia*, marks the probable site of attachment of a bodenaponeurosis (Fig. 1D, att apon) serving for the insertion of much of that part of the external adductor described above. This function for the coronoid eminence is indicated by comparisons with living reptiles (Barghusen 1973) and is consistent with direct evidence of tendon attachment in *Dimetrodon* (Barghusen 1968) and theriodont therapsids. A similar insertion would also have been present in all dinocephalians (Fig. 4C, att apon) and, as Cluver (1975) has

recently pointed out, in dicynodonts, in which the posterodorsal tip of the dentary marks a site of tendinous attachment (Fig. 3C, att apon) identical in position to that in *Venjukovia*.

By far the most important question concerning the external adductor in *Venjukovia* is whether or not a lateral division was present comparable to that found in dicynodonts (Figs 2D, 3B, C). The external adductor jaw musculature independently established an extensive area of attachment on the zygomatic arch and exposed lateral surface of the lower jaw at least twice and probably three times in therapsid history. This definitely occurred in cynodonts (Barghusen 1968) and dicynodonts (Watson 1948; Crompton & Hotton 1967; Cluver 1975) and probably occurred in gorgonopsids (Barghusen 1968; Kemp 1969). In each group the manner in which this muscular modification occurred is highly distinctive. In cynodonts a laterally bowed zygomatic arch created a channel through which developing masseter musculature descended from the temporal fossa to insert on the lateral surface of the dentary; subsequent events led to the establishment of muscular origin on the entire zygomatic arch. An invasion also occurred in gorgonopsids but in this case the muscle attachments were confined to the lateral surface of the angular and the posterior root of the zygomatic arch. In dicynodonts, a channel was created for the invasion of musculature from the confines of the temporal fossa through the dorsal displacement of the zygomatic arch relative to the dorsal surface of the lower jaw (Crompton & Hotton 1967). This invasion resulted in a newly added lateral division of the external adductor originating from the arch and expanded lateral surface of the squamosal and inserting on a distinctive lateral shelf of the dentary (Crompton & Hotton 1967; also see Figs 3B–C). This muscular development is a dicynodont hallmark, as is the developing masseter muscle for cynodonts.

Despite the limitations of incomplete preservation posteriorly, the morphology of *Venjukovia* indicates that this animal closely conforms to, and may reflect, an initial stage in the development of the condition seen in dicynodonts. The zygomatic arch is dorsally displaced relative to the jaw articulation. This created the necessary condition whereby external adductor musculature originating on the ventrolateral part of the posterior wall of the temporal fossa (the quadratojugal and quadrate as reconstructed in *Dimetrodon* (Barghusen 1973)) had free access to invade the lateral surface of the squamosal by a route passing inferior to the level of the zygomatic arch (Fig. 2). It is also apparent (Fig. 2) that the zygomatic arch of *Venjukovia* and dicynodonts was dorsally displaced to the level of the inferior margin (Fig. 2A, inf mar) of the attachment of the external adductor to the inner surface of the cheek as reconstructed in *Dimetrodon* on the basis of stretch capabilities of muscle (see Barghusen 1968). This suggests that much of the length of the inferior and medial surfaces of the arch could have served for the origin of musculature with sufficient fibre length to allow for a substantial gape (also see Watson's 1948 discussion of gape in dicynodonts). Finally, this displacement removes the zygomatic arch from

immediate proximity to the lateral surface of the lower jaw which, thereby, becomes a potential site of muscle insertion.

The extent of invasion of muscle attachment onto the lateral surface of the squamosal is impossible to determine in *Venjukovia* due to insufficient preservation of the posterior root of the zygomatic arch. However, the presence of a fossa (Fig. 1C, fossa) excavated into the lateral surface of the surangular and most posterior part of the dentary, as a departure from the primitive therapsid condition, strongly suggests that such invasion did take place. The fossa indicates the incipient development of muscle attachment to the dorso-lateral surface of the jaw corresponding to the insertion of the lateral division of the external adductor in dicynodonts (Fig. 3C); the insertion has merely expanded anteriorly in dicynodonts to include more of the dentary. The fossa thus indicates the presence of a laterally placed muscle whose area of origin may well have included the lateral surface of the squamosal. If so, the impression of the squamosal left on the matrix suggests that the posterior root of the zygomatic arch was shaped as in Figure 1C and capable of supporting an area of origin from its lateral surface as is illustrated.

M. ADDUCTOR MANDIBULAE INTERNUS PTERYGOIDEUS (POSTERIOR)

The area of origin of the posterior pterygoid muscle in *Venjukovia* is clearly very similar to that reconstructed in *Dimetrodon* (Barghusen 1973). A boss on the distal end of the transverse process of the pterygoid as well as indications of a medial pterygoid crest (Fig. 1B, m pt cr) provide direct evidence of tendinous attachment in the manner of sphenacodontids, theriodonts, and brithopodids (Fig. 4B), as well as many living reptiles. The ventral surface of the quadrate ramus of the pterygoid is also expected to have served as an area of origin for this muscle mass (Fig. 1B, MAMIpt (post)). The major difference in area of origin of the posterior pterygoid muscle between *Venjukovia*, on the one hand, and *Dimetrodon* and brithopodids, on the other, is that the transverse process is less massive and projects anterolaterally in *Venjukovia* (cf. Figs 1B, 4B). The anterolateral projection approaches (but by no means achieves) the condition in dicynodonts, in which the transverse process has lost its role in bracing and controlling the movements of the lower jaw and projects almost straight forward (Fig. 3B, tp). In this regard, *Venjukovia* resembles a morphological stage which was probably antecedent to the condition in dicynodonts.

It is generally assumed that the transverse process of the pterygoid is either reduced (Romer 1956) or entirely eliminated (Watson 1948; Crompton & Hotton 1967) in dicynodonts. It appears, however, that this structure is merely redirected forward and in many cases is well developed. The structure labelled as the transverse process in Figure 3B has the same general topographic relationships to the subtemporal fossa and the ectopterygoid (when the latter is present) as does the structure which is clearly the transverse process in *Venjukovia*. Moreover, direct evidence in one acid-prepared specimen (SAM-4325) of *Lystrosaurus* indicates that the relationship to the posterior pterygoid muscle

is also the same. The ventral surface of the distal portion of the process is slightly rugose and striated, suggesting tendon attachment. In addition, a line of parallel striations (Fig. 3B, str) extends posteromedially from the ventral edge of the anteriorly directed process to terminate near the level of the basipterygoid joint. The position of this line corresponds to that of the medial pterygoid crest and also provides direct evidence of probable tendon attachment.

The area of insertion of the posterior pterygoid muscle in *Venjukovia* (Fig. 1B) is expected to have included the ventromedial surface of the articular and probably the anteromedial face of the retroarticular process. This reconstruction contrasts with many made in the past in which it was assumed that pterygoideus musculature ran beneath the jaw to insert on the lateral surface of the main body of the angular medial and posterior to the reflected lamina. This has been thought to have been the case in spheonodontid pelycosaur and in therapsids in general (see Barghusen 1968, 1973; Crompton & Hotton 1967; Watson 1948). The muscle involved has been given various names and reconstructed with a number of different areas of origin; however, it is the posterior pterygoid muscle as reconstructed by Barghusen (1973). While an insertion on the lateral surface of the angular appears to be valid for spheonodontids, its validity is questionable in most therapsids. As pointed out by Allin (1975), the very close relationship between the reflected lamina and the lateral surface of the main body of the angular in the vast majority of therapsids, including brithopodids, *Venjukovia*, and dicynodonts, argues against the intervention of musculature between these structures. The confinement of musculature within such a narrow space would cause functional inefficiency since the amount of muscle is necessarily very small and, as Allin remarks, the muscle 'would be unable to shorten without bulging against its skeletal confines as well as constricting off its own blood supply, although an associated venous plexus might provide volumetric compensation'. It may be added that if a venous plexus were present in the space between the lamina and main body of the angular, the amount of musculature present would have been negligible. It is more reasonable, as persuasively argued by Allin, to regard this space as housing an air-filled chamber existing as a tympanic or pharyngeal diverticulum and functioning in sound reception.

CONCLUSIONS

The pattern of adductor jaw musculature reconstructed for *Venjukovia* suggests that this animal is closely related to dicynodonts—perhaps more closely related to dicynodonts than to any other known therapsid group. A close relationship is indicated by: 1. the probable presence of a similar lateral division of the external adductor in both groups in contrast to the condition in other therapsids; and 2. the fact that the structure of the area of origin of the posterior pterygoid in *Venjukovia* is consistent with the structure postulated for a theoretical morphological stage transitional to the dicynodont condition. The muscular morphology of *Venjukovia* contrasts with that of

primitive dinocephalians in that there is no specialized origin of the external adductor from the dorsal surface of the temporal roof in *Venjukovia*. Unless a reversal (i.e. secondary elimination of this area of origin) is postulated, animals which would be classified as dinocephalians were not involved in the ancestry of *Venjukovia*. At the moment, there is no evidence which suggests that such a reversal took place. The therapsid ancestry of *Venjukovia* is, the author believes, an open question.

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REFERENCES

- ALLIN, E. F. 1975. Evolution of the mammalian ear.—*J. Morph.* **147**: 403–438.
- BARGHUSEN, H. R. 1968. The lower jaw of cynodonts (Reptilia, Therapsida) and the evolutionary origin of mammal-like adductor jaw musculature.—*Postilla* **116**: 1–49.
- BARGHUSEN, H. R. 1973. The adductor jaw musculature of *Dimetrodon* (Reptilia, Pelycosauria).—*J. Paleont.* **47**: 823–834.
- BARGHUSEN, H. R. 1975. A review of fighting adaptations in dinocephalians (Reptilia, Therapsida).—*Paleobiology* **1**: 295–311.
- BOONSTRA, L. D. 1963. Early dichotomies in the therapsids.—*S. Afr. J. Sci.* **59**: 176–195.
- CLUVER, M. A. 1975. A new dicynodont reptile from the *Tapinocephalus* Zone (Karoo System, Beaufort Series) of South Africa, with evidence of the jaw adductor musculature.—*Ann. S. Afr. Mus.* **67**: 7–23.
- CROMPTON, A. W. & HOTTON, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida).—*Postilla* **109**: 1–51.
- EFREMOV, I. A. 1940. Preliminary description of new Permian and Triassic terrestrial vertebrates from the U.S.S.R.—*Trudy paleon. Inst.* **10**: 1–140.
- KEMP, T. S. 1969. On the functional morphology of the gorgonopsid skull.—*Phil. Trans. R. Soc. (B)* **256**: 1–83.
- OLSON, E. C. 1962. Late Permian terrestrial vertebrates, U.S.A. and U.S.S.R.—*Am. phil. Soc. Trans.* **52**: 1–224.
- ORLOV, J. A. 1958. Predatory dinocephalians from the fauna of Isheyevo (Titanosuchia).—*Trudy Paleon. Inst. Akad. Nauk.* **72**: 1–114.
- ROMER, A. S. 1956. *Osteology of the reptiles*. Chicago: University of Chicago Press.
- WATSON, D. M. S. 1942. On Permian and Triassic tetrapods.—*Geol. Mag.* **79**: 81–116.
- WATSON, D. M. S. 1948. *Dicynodon* and its allies.—*Proc. Zool. Soc. Lond.* **118**: 823–877.

ABBREVIATIONS

an	angular
art	articular
att apon	attachment of the bodenaponeurosis
bo	basioccipital

bs	basisphenoid
d	dentary
ect	ectopterygoid
f	frontal
inf mar	inferior margin of the origin of the external adductor from the inner surface of the cheek
j	jugal
l	lacrimal
m	maxilla
MAME	external adductor muscle
MAME (lat)	lateral division of the external adductor muscle
MAME (med)	medial division of the external adductor muscle
MAMIPt (post)	posterior pterygoid muscle
m pt cr	medial pterygoid crest
n	nasal
p	parietal
pal	palatine
par	paroccipital process
part	prearticular
pf	postfrontal
pm	premaxilla
po	postorbital
prf	prefrontal
pt	pterygoid
q	quadrate
sa	surangular
sm	septomaxilla
sp	splénial
sq	squamosal
str	striations
temp cr	temporal crest
tp	transverse process of the pterygoid
v	vomer
Nat. Mus.	National Museum, Bloemfontein, South Africa.
PIN	Palaeontological Institute, Moscow, U.S.S.R.
SAM	South African Museum, Cape Town, South Africa.

6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers, date and geographical positions.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.



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A PRIMITIVE ANOMODONT THERAPSID
FROM THE PERMIAN OF THE U.S.S.R.